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THE NATURAL HISTORY, ORGANIZATION AND LATE
DEVELOPMENT OF THE TEREDINIDAE.

A Thesis

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of the Johns Hopkins University for the Degree of
Doctor of Philosophy.

by

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Introduction.

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My work on the "Ship-worms" was first suggested by Professor W. K. Brooks. His constant interest and sympathy throughout my stay at the Johns Hopkins University have been of great help to me and it gives me great pleasure to acknowledge my indebtedness to him. My material was collected at Beaufort, North Carolina, during the summers of 1895 and 1896, and my study has been continued in the laboratory in Baltimore. To the Authorities of the Johns Hopkins University I am under deep obligations, both for the privileges of the marine laboratories at the seaside, and for facilities for work in the laboratory in Baltimore.

The "Ship-worms" were favorite objects for study during the eighteenth century, on account of their great damage to the dykes of Holland in 1733 and subsequent years. The first modern observations were those of Valisnieri (1715) and Deslandes (1720). After 1733, came Mossuet, J. Rousset, and especially Godfrey Sellius. These observers seem to have been unaware of the ancient observations mentioned by Theophrastus, Pliny and Ovid, and it was supposed the "Ship-worms" were natives of India, whence they had been brought

by shipping in modern times. It was Godfrey Sellius who first recognized the Molluscan characters of *Teredo*, but these were not used by Linnaeus, who grouped it along with *Serpula* and *Dentalium*. Cuvier and Lamarck adopted the view of Sellius, and since their time the group has been put in its proper place.

The first reliable observations on the anatomy of the "ship-worms" were those of Deshayes, who gave a number of beautifully executed plates to *Teredo* in his "Mollusques d'Algerie", 1846. However, like most of the plates of this great work, they are difficult to study and interpret. Supplementing the work of Deshayes is that of Quatrefages, (14) who began and completed his observations before he had access to the published results of Deshayes. This "Memoire sur le Genre Taret (*Teredo*, Linn.)" is the one usually cited at the present time, although the paragraph with which Quatrefages prefaces his paper is almost as applicable now (with slight changes in the wording) as when it was written in 1849. "Naturalists up to the present time", he says, "have strangely neglected *Teredo*. This is not the place to review the anatomical researches of the last century which are filled with errors excusable by the state of science of that

period. But it is surprising that a mollusc with such remarkable external characters has not been the object of any special research from the foundation of comparative anatomy up to the present time. It is necessary to come to the year 1846 to find a naturalist who has taken for the subject of his observations this mollusc so unfortunately celebrated.

Since the appearance of the memoir of Quatrefages, no detailed account of the whole organization of *Teredo* has appeared. Only in comparative treatises has it been taken up. The principal of these are the papers by Grobben (4) on the pericardial glands in Lamellibranchs, by Menegaux (11) on the circulatory system in Lamellibranchs; and by Pelseneer (14) in his extensive comparative studies in the group. Grobben first observed the anterior adductor muscle in *Teredo* and proved the *Teredinidae* to be dimyarians. Aside from this point, the figure of *Teredo* that he gives is wholly unreliable. Menegaux attempted to establish the homologies of the aortae, and Pelseneer described the visceral ganglion and related structures. I shall have occasion to refer to these papers in special parts later, and it will be seen that the comparative method of study is not always satisfactory, if the examination of special forms be not made with

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sufficient care. My results differ from all of these. Unfortunately the first two do not state the species on which they worked, and so I cannot state that where my observations differ from theirs, they were in error, though there is such great uniformity of organization in the various species, that we may expect only differences in detail in the various types.

My observations have been based chiefly on *Xylatrypa fimbriata*, Jeffreys, and unless otherwise stated, this is the form described and figured. Specimens of this species I have had in all stages of development from the newly attached larva to the adult. I have also studied *Teredo navalis*, Spengler, and *T. navalis*, Linne and where these are essentially different or more favorable for description, they have been used. In general, where "Teredo" is used as a popular term, it applies to *Xylatrypa* as well as to the species of *Teredo*, in a strict sense.

The object of my study of the "Ship-worms" has been two-fold. In the first place, I have endeavored, by the use of modern methods, to give a detailed account of the organization of this highly specialized Lamellibranch and to correct the errors that have heretofore existed in the

descriptions of it. In the second place, by the study of young stages, I have been able to trace the transformation of the typical Lamellibranch larva into the highly specialized "Ship-worm".

I have also traced the early embryology on the artificially fertilized eggs of *N. limbriata* and *T. norvegica*, in both of which the eggs are laid free into the water. Stages later than the typical Lamellibranch veliger raised in aquaria, I have not been able to observe. The intermediate stages, between these and the newly-attached larva, I hope to observe on the larvae of some viviparous species at a future time, so as to complete my study of the development from the egg to the adult.

II. METHODS.

My preserved material was collected and prepared for study as follows:- By hanging boxes and other structures of wood in the water at Beaufort, I was able to obtain all stages from the newly-attached larva to "lip-worms" four inches long, with adult organization. The youngest stages were collected from the surface of the wood. Later stages were dissected out of the wood into which they had bored. Early stages were narcotized with cocain and afterwards fixed with mercuric chloride. Specimens 1 cm. or more in length were treated as follows: They were exposed quickly and immediately a quantity of Hermann's solution was dashed upon them. This kills them instantly, before they have had time to contract appreciably. They were then immediately immersed in mercuric chloride or Perenyis' solution for fixation. After washing in weaker alcohols, specimens were preserved in 90% alcohol. The early stages were stained in Kleinenberg's hematoxylin. For later stages, the best results were obtained with borax-carmin, followed by Lyons blue. For the examination of whole objects, the best results were obtained by staining in a weak solution of borax-carmin in acid (1-2% 21.) 70% al-

cohol, which decalcifies as well as stains. The figures have all been drawn with the aid of a Zeiss camera lucida. In some cases, as in the series of transverse sections of the adult (*Fig. 1-10*), they have been "touched up" afterwards. However, in no case have they been essentially modified and are in no wise diagrams. The figures of adults have been made from specimens about ten centimeters long, which I had raised, and which were killed perfectly extended. The siphons, however, have been filled in from life, or from preserved specimens that had been narcotized before killing. In larger specimens the body as a whole, and the various organs are somewhat more elongated, but the relations remain the same as in younger specimens.

III. NATURAL HISTORY OF THE "SHIP-WORMS".

Any wooden structures that one may examine at Beaufort, which have been in the water for some time and unprotected, are always found infested with "Ship-worms". These are of three species, which Professor W. H. Dall has kindly identified for me as *Xylotrya fimbriata*, Jeffreys, *Teredo navalis*, Linne and *T. norvegica*, Spengler. *X. fimbriata* and *T. norvegica* are very abundant, while *T. navalis* is found but rarely. *X. fimbriata* is the most abundant of all, and is found everywhere. It may attain a length of two feet, though where it grows in large numbers it is so crowded that specimens are oftener less than a foot in length. *T. norvegica* I have found mostly in the heavier piles of wharves, where specimens may attain the great size of four feet in length and an inch in diameter. *T. navalis* I have found very sparingly, not over a dozen specimens among the thousands of individuals I have examined. These in all cases were small specimens, from which it seems that the habitat at Beaufort is not favorable for them, and is more favorable for the other two species which fully occupy all of the available places for ship-

worm" life. The water contains a high percentage of salt, and the warm season is long, and these factors may account wholly or in part for the absence of *T. navalis*.

Of the thousands of young specimens (under four inches in length) I have taken from boxes, all were of *T. fimbriata* except four specimens of *T. navalis*. These were observed in June, July and early in August. Whether the absence of *T. norvegica* was due to unfavorable locations, or the season for attachment is different from that of the other two species, I was not able to determine.

Breeding Habits. As is well known, some species of *Terebratulina* do retain their eggs in the gills during the embryonic development. This is true of *T. navalis*, and even the small, (an inch or more) specimens of this species I have taken, have usually had embryos in various stages of development. On the other hand, I have found that the eggs of the other two species are laid free into the water. If species of *T. Norvegica* be taken from their tubes, they soon begin to extrude their sexual products, if these be mature. The eggs and sperm are extruded from the anal or exhalent siphon in a slow, steady stream, which continues

as long as the sexual organ contains ripe sexual products. *Polotrya fimbriata* I have observed but rarely extruding its sexual products in this manner, but why there is a difference in this habit I have not determined.

In accordance with their free development in the water, the eggs of the "Whip-worm" are very small and very numerous. While they vary somewhat in size, they have an average diameter of somewhat less than 1-20 mm. Very large specimens may lay great numbers of eggs at one time; in one case I estimated the number laid by a large female of *T. norvegica* at one hundred million. The sperms are very minute, and much more numerous than the eggs. The eggs of both species that lay their eggs free may be fertilized artificially, and pass the early stages of development with great uniformity and rapidity in aquaria. The eggs when first laid are of irregular shapes. They soon become spherical, and if fertilized, the polar bodies are soon extruded and segmentation begins. Development is very rapid and on warm days, the embryos become free-swimming within three hours after the eggs are laid. Within a day the shell has been formed and the typical Lavelle-branch veliger stage is reached. Beyond this stage they

do not develop in aquaria, though they may live for days afterwards. Hatschek has observed (6) that the Viviporous larvae of a species studied by him (*T. navalis*?) are almost always present in only a few stages, and that transitional stages are but seldom found. It seems probable that the free-living larvae of *Xylotrya* and *T. norvegica* attain one of these stages within a short time, and that the unusual conditions in aquaria prevent their advance beyond it.

The mode of life, and rate of development beyond the early stage attained so rapidly in aquaria, have not been determined. What becomes of the larvae that hatch from the eggs, how and where they live, it is difficult to surmise. Though the developed larvae are settling on wooden structures constantly, I have not taken them and intermediate stages in the tow-net, and where they develop I do not know. However, the rate of growth of the marine Lamellibranchs is slow, and I think the larvae of "Shipworms" that attach must be at least a month old, it may be more. At this time their development is quite advanced and their organization complex. (The organization of the organization of the larvae)

The breeding season of *S. limbrata* and *P. norvegica* seems to extend through the warm season. I have found ripe sexual products of both species from early in May till the middle of August. At the latter time there seemed no abatement in their development. As will be described later, individuals became sexually mature in a month after they have attached, and those which attach in August must bear ripe sexual products later in the season, so that the breeding season seems to extend through the summer.

Attachment of the Larva.- During its free mode of life, the "ship-worm" larva has gradually developed into the typical larva of marine Lamellibranchs. There is a shell into which the whole creature may be withdrawn for protection; a large swimming organ, the velum, by means of which the larva swims freely in the water; a long, active foot, by means of which it crawls actively over surfaces. At the end of this larval development, in fact, the "ship-worm" larva is a typical small bivalve, except that it possesses the swimming organ.

Throughout the summer (or at least from May till

August) at Beaufort, if one examines unprotected wooden structures submerged in the water very small bivalves will be found crawling actively over the surface. These are very minute and are easily recognized as "Ship-worm" larvae that have just settled upon the wood. The larva moves rapidly in search of a favorable place for attachment, and this is usually in some minute depression or crevice in the wood, though it may also become attached to perfectly smooth surfaces. It seems to possess no organ of special sense for the purpose, and yet, it is able to determine what places are favorable for its future life, and to avoid those which are not. Once it has chosen a point for attachment, it throws out a single long byssus thread, which secures it at the surface of the wood, and soon loses its velum, so that it can no longer lead a free life. Once attached, the larva begins to clear away a place, by scraping away the surface of the wood with the ventral edges of its shell valves. Small particles of wood and other substances, that are thus formed, are cemented together over the larva so as to form a sort of conical covering for protection. This, the transformation of the larva into the small "Ship-worm" begins and progresses rap-

idly. The foot becomes a pestle-shaped organ which assists the shell in burrowing. The shell valves lose their power of opening at the ventral side, and by the development of knobs on the ventral and dorsal portions of either valve, they are able to swing on each other at right angles to the former direction. Meanwhile the shell gapes at both anterior and posterior ends, for the protrusion of the foot in front, and the siphons, and later the body, behind. And on the anterior edges have been formed the small teeth which at this and later stages are the mechanical agents by which their possessor bores into the wood. This transformation has taken place within two days from the time the larva has settled, and afterwards the animal rapidly becomes a "Ship-worm", enlarging its burrow in the wood as it increases in size.

Rate of Growth within the Wood.- The "Ship-worm" in its larval stages develops but slowly, but once in the wood, it grows with remarkable rapidity. During its free life, most of its energies seem devoted to active locomotion and development; after attachment, it leads a sedentary life and its growth is correspondingly rapid. The newly-attach-

ed larva is somewhat less than .25 mm. long. In 12 days it has attained a length of about 3 mm.; 16 days, 6 mm.; 20 days, 11 mm.; 30 days, 63 mm., and 36 days, 100 mm. It is thus seen that within two weeks from the time it has settled, the "Ship-worm" has increased hundreds of times in size, and in five weeks, thousands of times. Within two weeks it has changed to a real "Ship-worm", and even in a month specimens may contain ripe sexual elements, though normally these are retained till larger quantities of sperm and eggs are stored for extrusion at one time. I shall describe later what appears to be a change of sex from males to females, the male sex being developed in young specimens. I have found males four weeks old gorged with ripe sperms, and in every way adult.

The ages of larger specimens I have been able only to estimate, from the time the piles and other wooden structures from which they were taken, had been in the water. In one case I took specimens four feet long and an inch in diameter at the anterior end, from piles that had been in the water less than two years. This was in July, and in this case it seems the "worms" had entered the wood not earlier than the spring of the preceding year, and

hence were little if any over a year old.

The rate of growth seems to depend but little if at all, on the hardness or kind of wood. It is well known, "Ship-worms" penetrate all kinds of wood, whether it be soft white pine or hard oak. In India there are types that bore into stiff clay. None of our species adopt such a habitat, so far as I know. But I have found small, abnormal specimens of *Xylophaga* in very rotten wood, and I take it that their abnormal character was due to unusual conditions. In this case they were associated with *Xylophaga corsalis* and *Pholas dactylus*. However, in wood proper, I have observed that they grow quite as rapidly in hard yellow pine as in soft white pine; so that the rate of growth seems conditioned by food supply, and not by the ability of the animal to form its burrow.

Protective Adaptations. - The life of the "Ship-worm" in the wood has led to profound changes in the character of its external parts and its means of protection. As the "worm" enters, the posterior part of the body projects more and more beyond the shell which loses its protective

character, to take upon itself the sole purpose of burrowing. In specimens 2 mm. long, the shell is still a quarter of the length; in specimens four feet long, the shell is an inch or less in length. With the loss of protection by the shell, other means are acquired. In a general way, the burrow offers the protection afforded by the shell in other forms. But the very delicate tissues of the mantle would be injured by the rough surface of the wood, and so as the body elongates, it secretes around it a constantly thickening calcareous tube, which lines the whole burrow except the anterior end, where the mantle is somewhat less delicate; and where the tube fades out and the burrow is being constantly enlarged.

When the young "worm" enters the wood, it penetrates vertically to the surface, but soon bends its course, so that within two inches, usually, it becomes straight and the worm bores with the grain. Individuals that enter the wood on end, cut across the grain from the start, so that their burrows are straight, unless they are turned from their course by obstructions of any sort. If these are met, the course is changed so that the burrows may become very tortuous. When the "whip-worm" is in danger of bor-

ing into the tubes of its fellows, or into other spaces, if its course can be no longer changed, it contracts the anterior part of the body slightly, secretes a closed calcareous lining in front of it, and ceases to burrow further and to grow. Otherwise, it seems it may grow indefinitely, and it is difficult to predict how large specimens of *T. norvegica* might become, were there not adverse conditions to stop their growth.

I believe the calcareous lining of the burrow has been acquired primarily for the protection of the very delicate body from the rough surfaces of the wood. But it serves other purposes also. It prevents the diffusion of injurious substances into the burrow, and also prevents the intrusion of other creatures that live in the wood. Then, too, when the surrounding wood decays, or is eaten away by other animals, so as to endanger the life of the "ship-worm", the tube may be so strengthened as to serve as the sole means of external protection. In this way the walls of tubes which, protected, are usually not over a quarter to a half millimeter thick, may become two millimeters or more thick. This response of the animal to changed conditions on the outside is a very mysterious one.

and it is difficult to see by what means it recognizes its danger.

The peculiar mode of life of *Teredo* has led to the development of the palettes (fig. 10). These are protective structures peculiar to the "Ship-worms". They differ somewhat in the various species, but are essentially calcareous paddles, attached one on either side of the posterior end of the body. In *Xylotrya* the paddle part consists of a series of funnel-shaped calcareous structures, set one within the other upon a cylindrical handle, while in *Teredo* it is composed of a single piece. The handle of the paddle is imbedded in an invagination of the mantle and the paddles project freely behind, where by means of a set of muscles, they may be protracted forcibly so as to completely close the outer end of the burrow, against the intrusion of any enemy from the outside. Also, when the burrow extends upwards and is more or less exposed at low tide, the palettes may so hermetically close the external opening as to retain the water in the burrow, and to prevent the collapse of the body of the "Ship-worms". The position of the palettes is shown in figures 11 and 12. When

the animal is feeding, the palettes are drawn forwards and the siphons are extended freely into the water, as shown in fig. 31. When it is disturbed in any way, the siphons are contracted very quickly and the palettes forced into the end of the tube as shown in fig. 32.

Mode of Burrowing.- The manner of mechanical formation of the burrow has been one of the most debated questions in the natural history of the "ship-worms" and their allies. In *Teredo*, various structures have had this work assigned to them, by various observers. In some cases the observers thought some chemical solvent to assist the mechanical action by softening the wood. Hancock thought there were siliceous particles in the mantle, to do the work. He probably observed the teeth as yet unattached to the shell. Quatrefages thought it the "cephalic hood", aided by some chemical solvent. This structure he described as muscular though it is but little muscular and could do no such important work as he assigned to it. Jeffreys thought it the foot, which by other observers was described as wholly absent. Osler, in 1826, had suspected the real mode of formation, though he did not actually observe it. The

The shell is the agent, assisted by the foot, as I have actually observed in young specimens under the microscope. The whole structure of the shell and the arrangement of its adductor muscles indicate this mode. The teeth on the anterior edges of the valves point outwards and backwards. On both dorsal and ventral portions of each valve (figs. 12 and 13) there are stout calcareous knobs, which form a double pivot by which the valves swing upon each other, by the contraction of the adductor muscles. The mode of burrowing is as follows: While the foot performs a cupping action, so as to draw the shell close against the surface of the wood, the posterior adductor muscle contracts, so that the teeth on the shell rasp away the wood. The valves are brought to the original position by the small adductor. The comparatively very large posterior adductor is therefore the active agent that does the work, aided by the foot; the shell is the tool by which it is done.

Ingestion of Wood and Food.— As in other Lamellibranchs, a constant stream of water is passing through the siphons when they are extended into the water, which serves for respiration and also contains the small organisms which

serve for food. These consist mainly of diatoms and simple floating algae, and other minute organisms. Small crustacea and other animal forms seem almost never eaten.

The particles of wood that are rasped away in forming the burrow are ingested, as the only means of getting rid of them. It has often been debated whether they undergo any digestion in the alimentary canal, and I am inclined to think they contribute something to the nutrition of "Ship-worms". Boring I think to be a periodical function, perhaps alternating with more active ingestion of food. This is indicated by two facts. In the first place it seems that while the teeth are being cemented to the anterior edges of the valves, the shell could not be used. Also, the caecum of the stomach contains mainly particles of wood, which indicates that while burrowing, the orifice into it is open. The caecum contains a very large fold of the internal membrane (figs. 1-2) and seems so eminently an absorbent structure, that for this reason it seems to me there must be some action on the particles of wood within it.

IV. ORIGIN AND EARLY DEVELOPMENT OF THE "SHIP-WORMS."

a. The General Organization.

In their form and general organization, the adult "ship-worms" are the most peculiar and striking of all the Lamellibranchs. Their newly-attached larvae have the form and most of the organization of the larvae typical of most of the marine Lamellibranchs, which are free-swimming during their larval development. The transformation of the typical larva into the highly specialized "ship-worm" takes place with such great rapidity as to properly be called a metamorphosis.

The Larva and its Metamorphosis. - The general shape of the newly-attached larva (fig. 1) is that of a small clam, with equal shell valves. These latter are broader than long, so that this Lamellibranch which has a more elongated adult, has a larva more fore-shortened perhaps, than any other form. The youngest specimens I have found were creeping over the surface of the wood by means of their very active, tongue-shaped foot. The velum was in all cases retracted into the large velar cavity (v.c.), a large space in the anterior, dorsal part of the shell cavity, well shown in fig. 21, which is a sagittal section

of a newly-attached larva. The foot (figs. 1, 2, 3) at this stage is very long, ciliated over most of its extent, and angular at its posterior end. This angular portion is occupied by a well developed, though simple byssus apparatus, which throws out a single, simple byssus thread, several times as long as the diameter of the larva. This serves to secure the larva in the early stages of attachment, so that, after the velum has been lost, it may still return to its mooring if it lose its footing from any cause.

The siphons are already well developed in the larva, the ventral (i. e. figs. 1, 2, 3) with ciliated sensory papillae, the dorsal (fig. 4), a simple non-ciliated tube. The gills have advanced but little beyond the stage figured by Matschek (6) for the viviparous larva studied by him. On each side of the body there are two large gill-slits, one in the gill membrane, the rudiment of a third. The "worm" larva is a typical dimyarian. Both adductor muscles are present in their usual positions, the posterior (fig. 5), already larger than the anterior (fig. 6). The processes of the foot at this stage are attached in the umbral region of the shell just in front of the poste-

rior adductor.

The alimentary canal is already highly specialized (Figs. 1, 38). A comparatively long oesophagus (o.e.) leads into the stomach, from which a single large liver vesicle projects on either side. The sheath of the crystalline style projects from the posterior ventral portion of the stomach on the midline. The intestine leaves the stomach from the right side, anteriorly, and the caecum peculiar to the Pholadacea is present as a hemispherical rudiment on the right side, just posterior to the opening of the intestine.

The nervous system of the larva (Figs. 1, 39) is highly specialized. The ganglia are composed of ganglion cells and the connectives contain only nerve-fibres. On either side the pleural (pl) ganglion is still separate from the cerebral (c). Between the pleural a connective passes to the visceral, and from the cerebral, one to the pedal. I think a pleura-pedal connective is also present, but this I am not able to state positively. The two pedal ganglia are closely fused, while the visceral are wide apart.

The kidneys (k.) (Fig. 40) consist of large vacuolated

cells, and open externally in front of the posterior adductor. The internal, pericardial openings I have not been able to find. Lying around the cerebral ganglion is a gland, which so far as known, is peculiar to "shipworms" and which in later stages, becomes so greatly developed in connection with the gills. The glandular portion (F.D., fig. 5) contains spherical cells, and from it a duct opens to the exterior (A.D.) under the cerebral ganglion.

Metamorphosis. - The duration of the free-swimming life of the larva is not known, but it is perhaps a month, more or less. In a very much shorter period, the peculiar "shipworm" has been developed, with adult organization. The first change is the sudden, complete loss of the velum. Within a few hours after the larva has settled, the velum begins to disintegrate, and its constituent cells are cast off and eaten by the larva. The lower lip is projected forwards under the cavity of the velum, and as the cells are cast off, they cannot pass to the exterior, and so are eaten. The basement membrane of the cells of the velum contracts rapidly and the cavity of the velum is very

quickly obliterated (within a few hours).

Accompanying the loss of the velum, the long byssus thread has been secreted. As soon as the larva is secure, it seeks a place to burrow, and in preparation for its future life, its whole organization begins to change. The fusion of the mantle ventrally progresses rapidly, and within two or three days (fig. 3) only the opening for the foot is left. The siphons elongate rapidly and very early the mantle grows out so as to project beyond the shell. The latter changes rapidly after attachment. Within two days the first row of teeth has been formed on either valve; the greater growth on the ventral edges causes the two valves to gape for the protrusion of the foot; the knobs have been formed on dorsal and ventral portions; the apophyses have been formed and the retractor muscles of the foot have become attached to them. The foot, meanwhile, has become pestle-shaped.

The alimentary canal takes an important part in the general change. The caecum of the stomach, present in the larva as a rudiment, enlarges very rapidly, and even before woody material has been ingested in quantity, it projects as a large vesicle into the foot. In the early stage of attachment, 44 days after hatching, a half millimeter

long) it already forms a large part of a visceral mass. As the ingestion of woody materials progresses, the caecum projects more and more posteriorly, and in specimens 2 mm. long (Fig. 7), it extends much beyond the posterior adductor. The gills soon grow around the foot posteriorly and in specimens 2 mm. long, ten to twelve days old, project much beyond the visceral mass (Fig. 7). This same stage also shows the pericardial space, with its contained and associated structures, in the position which it occupies in the adult, distinctly posterior to the large adductor. And, in this, as in subsequent stages the visceral ganglion lies on the posterior end of the pericardial cavity.

There are a number of facts in the organization and metamorphosis of the larva that seem to have a wider significance. One of these is the sudden and complete loss of the velum. Iovin thought that, in forms studied by him, it entered into the formation of the labial palps. These structures are present in *S. cirrhiata* only as the small ridges on the sides of a slight groove around the mouth; so that a form in which they may be said to be absent, does not give necessary evidence against the derivation of the palps from the velum in forms in which the

former are well developed. However, the velum in various Lamellibranch larvae is very much larger than the palps in early stages, so that most of it must be cast off or absorbed. In the newly-attached oyster I have observed that the cells of the velum are absorbed more slowly, though, the palps are developed somewhat later merely as ridges on the sides of the mouth. The evidence from *X. fimbriata* and *O. virginiana*, it seems to me, shows conclusively that the palps are not derived from the velum. The loss of the velum is an event not confined to the Lamellibranchs. Wilson (17) has observed that the trochal cells of *Polysordius* are suddenly cast off and eaten as in *X. fimbriata*, and Pruvot has described the loss of the test in *Dondossia*. These all seem to be one and the same phenomenon, and indicate that the loss of a part of the ectodermal covering in these and many other forms is a very primitive and general occurrence.

The addition of the "lip-worms" to the forms which have heretofore been known to possess a byssus apparatus, indicates that this structure is perhaps universal in Lamellibranch larvae, though in the adult it may become degenerate. I may add that in *Ostrea virginiana* a byssus

apparatus is present in the newly-attached larvae, though here a secretion is thrown out for the attachment of the left valve, and does not form a byssus thread. In forms like *Teredo* and *Ostrea* the byssus serves for the attachment of the young bivalves, and apparently it has the same purpose in other forms in which it is present in the young (*Pecten*), but is lost in the adult. In *Sphaerium* it serves to attach the viviparous larva to the wall of the brood chamber. All the known facts go to show that the byssus-apparatus has been developed to assist in the transformation of the free-swimming pelagic larva into the bivalve with an attached or other settled mode of life; and that, the transformation having taken place, the byssus may be lost; or may be retained in forms which are permanently attached, but lack other means than the byssus for attachment.

The sheath of the crystalline style is well developed in the newly-attached larva. However, everything indicated its formation from the posterior end of the stomach. If we imagine the intestine leaving the blind end of the sheath, we get a form very like *Nucula* and *Valdia*, in which the posterior half of the stomach has the same

structure and function as the sheath in other forms, though no style is formed. As the intestine has left its median position at the extreme posterior end of the stomach in the development of more specialized forms, it has remained attached to various parts of the sheath of the style, as in *Capitum*, and has reached its greatest displacement in forms like *Teredo* and *Pholas*, in which it leaves the stomach from one side, and in which the sheath of the style forms a large blind pouch. If this view of the relations of the stomach, intestine, and sheath be the correct one, then the sheath is not a structure which has been acquired in the more highly specialized forms. It is homologous with the posterior part of the stomach of primitive forms like *Urcula* and *Yoldia*, while the intestine has left its original median attachment to the posterior end, to be attached to one side of, the stomach.

1. The General Organization of the Adult.

After the preceding description of the larva and its metamorphosis, the general plan of the adult "up-form"

will be easily understood. The body is covered by the mantle, which is 8-10. in. long. The body is covered by the mantle, which is 8-10. in. long. The body is covered by the mantle, which is 8-10. in. long. At the anterior end, on the left, the "head" is covered by the small shell, over whose dorsal and posterior portions duplicatures of the mantle project. Behind the shell, the long, naked body extends, tapering so that the whole "form" forms a truncated cone. At the posterior end are shown the points of attachment to the calcareous tube; and from it project the palloettes and siphons. From the anterior end, between the gapping shell valves, projects the pestle-shaped foot.

The naked, projecting part of the body is the mantle. If it is removed (fig. 9) the long gills are exposed posteriorly and the large visceral mass anteriorly. The latter is continuous with the foot and extends about two-fifths of the length of the body. It contains the viscera (digestive canal, genital organs, etc.). Dorsal to it lies the large pericardial cavity with its contents and associated structures (heart, kidneys, visceral ganglion). Dorsal to the pericardial cavity is the long, narrow anal canal, into which the rectum opens above

the posterior adductor muscle, and which is continuous with the epibranchial cavity behind the visceral anglion. The shell cavity is occupied mostly by the foot, and by the two adductor muscles which are common to most lamel-libranchs.

c. The Shell and Palettes.

The Shell.- The newly-attached "Ship-worm" larva possesses a typical bivalve shell. The valves are equal and united dorsally by a well-developed hinge apparatus. The shell in side view is wider than long; the transversal diameter is about equal to the longitudinal. The right valve (fig. 11) bears three equal hinge teeth; the left, two. Dorsal to the teeth is an external hinge ligament. In either valve, the apophyses of later stages is present as a rudiment. Up to this time growth has taken place along concentric lines. From this time on, rapid, very unequal growth in different parts of the valves causes a sudden transformation of the shell, which becomes very different from that of the typical bivalve. The initial stages in this change are shown in fig. 14, which is an anterior view of the shell of a "Ship-worm" which has been in the wood a day or less. After growing a small amount, the anterior border has cemented to it a row of teeth which have been secreted separately in small pockets in the epithelium of the anterior edge of the mantle. The first row of teeth, as well as those formed through life,

point outwards and backwards. The apophysis, present as a small rudiment in the larval shell, has grown out into the shell cavity, pushing the mantle invagination before it; and in this very rapidly attained stage, is almost as large comparatively as in the adult. Meanwhile, the ventral edge of the valve has grown rapidly, and there have appeared on the dorsal and ventral portions the two knobs, upon which the two valves swing in this and subsequent stages, during the mechanical process of boring. During these changes, the hinge teeth have disappeared, probably by absorption. The valves which, during larval life, have swung at the hinge so as to open or close the shell cavity on the ventral side, come to swing upon the knobs along a median transverse axis vertical to the axis of the hinge. The greater growth of the valves on their ventral edges causes them to gape before and behind for the protrusion of the foot and siphons.

Growth of the valves continues with great rapidity. The left valve of a specimen 1 mm. long is shown in oblique view in fig. 15. The chief features that have been introduced are as follows: The point of greatest growth is on the ventral edge. The line of growth, and hence the rows

of teeth, are wider apart on the dorsal half of the anterior border than on the ventral. In this way, an angle is formed, which soon (fig. 16) becomes a right angle. Meanwhile, the posterior border has grown rapidly and flares outwards so as to give better purchase for the posterior adductor during its contraction. Likewise, a much smaller portion of the dorsal anterior edge flares outwards for the attachment of the anterior adductor (fig. 18).

There is little modification in form or structure of the shell after the stage shown in fig. 16, which is a side-view of the left valve from a specimen 5 mm. long. As growth on the ventral edge takes place, the knob is constantly being added to towards the midline and absorbed on the side towards the concavity of the valve. And as growth at the posterior border takes place, the posterior adductor is constantly moving backwards. In the larval and subsequent stages, the whole shell, including the teeth, is covered externally by an epidermis.

The Palettes.- These structures are peculiar to the "Ship-worms" and have been acquired for the purpose of closing the outer ends of the burrow against intruders. The structure of one of these is shown in fig. 20, which

represents the left palette of a specimen 5 mm. long. It consists of a series of seven funnel-shaped structures which have been formed and cemented in succession to the handle. The formation of the palettes is as follows:-

In specimens still less than 1 mm. long, the mantle of the posterior region has formed a duplicature (figs. 4,7) which project over the base of the siphons. At the anterior portions of the sides of the space thus formed, the epithelium of either side pushes forwards. In the invagination thus formed, the handle of the palette is formed, and projects into the "collar" space. The lining walls of the sides of the collar space secrete the funnel-shaped pieces which are cemented to the handle. New larger pieces are added at the anterior end, and those first formed may be broken off. In *Teredo*, the paddle part of the palette is a solid piece and not divided into pieces, as has just been described for *Xylotrya*. Strictly speaking, the segments of a palette are semi-circular when seen on end. When the two palettes are brought together in closing the tube, they form a truncated cone.

d. The Mantle and Siphons.

In the adult "Ship-worm" (fig. 3) the mantle forms a very long and very delicate tube, which stretches from the anterior edge of the shell, to the ends of the siphons, which are modifications of the mantle, as in other forms of Lamellibranchs. This tube is open only at the anterior end, the pedal opening for the protrusion of the foot; and at the ends of the siphons, the inhalent and exhalent openings. It was formerly a much debated question, how much of this tube should be considered body proper, and how much siphons. In the light of our present knowledge, it is easy to see that the muscular collar marks off the end of the body and the beginning of the siphons.

The mantle of *Teredo* has undergone more differentiation than in any other Lamellibranch. The anterior edge is thickened, as in other forms, and secretes the teeth, the edges of the valves and the epidermis. The very delicate part underlying the shell and stretching to the siphons, secretes the inner layers of the shell, and the calcareous tube lining the burrow. Within the shell cavity, induplicatures secrete the apophyses and at the same time absorb part of them as they change shape and position.

also other parts secrete the two pairs of knobs on the valves. The posterior edge of the shell is not marked by the thickened mantle edge as in other types, but forms a duplicature around the whole posterior edge of the shell, which stretches forwards. In the dorsal region, the whole umbonal region of the valves is covered by this duplicature and to this special part, Quatrefages gave the name of "cephalic-hood" (c.h. figs. 7,28). To it he assigned the function of forming the burrow. It is somewhat, but not very muscular, and no such important work could be done by it. In the collar region it has been seen that the mantle forms the duplicature or collar which projects posteriorly over the base of the siphons; and within the cavity of which the handles and paddles of the palettes are formed separately (figs. 7,10). The siphons as part of the mantle, form two long tubes (figs. 7-9) which are fused together through half or more of their extent. The anal or exhalent siphon is without papillae or tentacles and is shorter and less muscular than the respiratory or inhalent siphon, which bears a number of tentacles (figs. 7-9). These are sensory structures, which also serve to close the entrance of the respiratory siphon very quickly.

Between the duplicature at the posterior edge of the shell and of the collar, the mantle is very uniform. Its structure is as follows:- Externally, the surface epithelium is composed of the flattened, non-ciliated cells, which secrete the calcareous lining of the burrow. Internal to the outer epithelium, are the weak muscles of the mantle, consisting of the longitudinal layer; a layer in which the fibres cross obliquely to the longitudinal fibres; and internal to these, the circular layer. The internal surface of the mantle (the lining of the mantle cavity), is lined by cells which in general are columnar and ciliated. Opposite the ends of the gills, the mantle is strongly ciliated and bears numerous mucous gland cells which empty to the surface. This region is indicated diagrammatically in figs. 29-34, where on either side ventral to the ciliated, glandular area the mantle wall is thickened, so as to form a groove opposite the groove of the gill.

Between the two epithelial layers of the mantle, there is a reticular net-work formed of connective tissue, with a small amount of muscle and nerve fibres, etc. The spaces so formed are lacunar blood spaces which are

filled by a peculiar substance whose nature I have not been able to determine. In living specimens the mantle is of a light grayish, translucent appearance. But specimens in alcohol become of almost a chalky whiteness, due to the masses of this peculiar material. Each lacunar space is filled by a more or less spherical nodule, which is just visible to the naked eye. Examined by transmitted light, these nodules are very opaque and seem composed of granular particles; by reflected light they are white. They are insoluble in acids, but soluble in water and quickly disappear in aqueous solutions. Deshayes described them as non-nucleated mucous cells. They are apparently the "siliceous particles" which Hancock observed, and with which he supposed the burrow to be formed. They are not cells, but deposits of some sort. It seems that they should be regarded as constituting a reserve of mucilaginous material of some sort for use as occasion may require.

Special Gland of the Mantle. - Lying between the two epidermal layers of the mantle, in the mid-dorsal region near the extreme posterior end of the body, there is a small special gland which is peculiar to the "Ship-worms".

Its position is shown in figs. 6 and 9; and its extent and structure in fig. 22, which represents a transverse section of the whole gland in a specimen about a half centimeter long. The gland consists of numerous, more or less spherical, vesicular acini whose average diameter is about a fortieth millimeter. They are lined by flattened, non-ciliated, slightly granular cells. From the gland a duct passes posteriorly to open on the dorsal outer surface.

This gland appears in the young "Ship-worm" soon after attachment as a single median small vesicle, of apparently epidermal derivation. As the animal grows, new vesicles are formed as outgrowths from those already present. What the function of the gland is, has not been determined, but its position indicates that it may be the secretion of a poison noxious to enemies that may get into the end of the "Ship-worm" burrow.

e. The Muscular System.

Early in this century it was one of the most debated questions in Zoology, whether the muscle then known in the "Ship-worms" was homologous with the anterior or pos-

terior adductor of other Lamellibranchs, or with both combined. It was Grobben who established the homology of the muscles when he discovered (5) the two small anterior adductor, which had been overlooked before.

In the general transformation of the larva into the "Ship-worm", the ligament, which in the larva opposes the two adductor muscles comes to serve only to keep the two valves from separating from each other. And the two muscles, which in the larva oppose the action of the ligament, to close the shell, come to cause the two valves to swing upon each other on the dorsal and ventral knobs of the shell valves, during the process of boring. So the two adductors become antagonistic to each other.

In the newly-attached larva, both adductors are present, the posterior (a.p. figs. 2, 24) already considerably larger than the anterior (a.a.). Both are attached in the concavity of the shell valve and well towards the dorsal side. In the general transformation, the adductor muscles as the active mechanical agents in boring, undergo considerable change. The posterior, as the one that really does the work, becomes very large (figs. 7, 9, 10), and passes posteriorly to be attached to the outwardly turned edges of

the shell (figs. 15-17) so as to give it better purchase during its contraction. The anterior, whose only work is to bring the shell valves back to their original position, after contraction of the posterior, is comparatively very small (figs. 7,9,10, a.a.), and moves forwards from the position in the larva, to be attached to the anterior, outwardly turned edges of the shell valves.

In minute structure, all of the muscle fibres of both adductors are apparently striated, due to a more or less regular deposit of granular material on their surface. This structure seems to support the view held of the two parts of the adductor in forms like Pecten. One part is tendinous and is supposed to prevent the shell valves from separating too far. The other part is for active adduction of the valves. In *Teredo*, where it is not necessary to oppose the action of a hinge ligament, all parts of both muscles are of the same character as that part in Pecten which is supposed to serve for active adduction.

The pedal muscles in the larva are those typical of Lamellibranchs with a foot. A pair of protractors of the foot are attached in the anterior umbonal region of the shell valves; and a pair of retractors, in the posterior

umbonal region, anterior to the attachment of the posterior adductor (r.p.e. fig. 26). With the remarkable appearance of the apophyses of the shell, the pedal muscles suddenly lose their old attachment in the umbonal region, to become attached to the apophyses through almost the whole length of the latter. After this shifting, which takes place as the young "Ship-worm" begins to bore, the pedal muscles no longer form distinct muscles, but wide bands which run from the apophyses to be distributed around the sides of the foot.

In *Teredo*, the posterior end of the body, which has usually been described as the "muscular collar", contains a number of highly specialized muscles, some of which are peculiar to the "Ship-worms". Their general arrangement, and their relations to the palettes and calcareous tube are shown in figs. 21 and 22. They are divided into two sets, those which manipulate the palettes, and those which are distributed to the siphons. The first set consists of a pair of protractors of the palettes (p.p.), two pairs of retractors of the palettes (r.p.) and a single adductor of the palettes (a.p.). On either side the protractor of the palette is inserted along the handle of the palette,

whence it radiates to be attached to the side of the calcareous tube along a broad line, its origin. On either side there are two retractors of the palette. One is inserted on the end of the handle and passes forwards to be distributed in the mantle along the sides of the body. The other is inserted near the outer end of the handle, whence it runs forwards to be attached along with the siphonal muscles. The adductor is a stout, cylindrical muscle, stretching between the anterior ends of the palette handles, and lying in the septum which divides the mantle cavity posteriorly. The muscles of the siphons are attached on either side along a triangular area to the calcareous tube, slightly anterior and ventral to the attachment of the palette muscles. From this origin the siphonal muscles are distributed to the siphons, mostly to the respiratory.

The action of the muscles of the palettes and siphons is as follows:- When the "Ship-worm" is undisturbed, the siphons are widely extended, as represented in fig. 21. If disturbed in any way, the siphons are retracted with great rapidity by the contraction of their muscles. At the same time, by the action of the protractors of the

palettes, the palettes are pushed forcibly into the end of the tube so as to completely close the latter. The outer ends of the paddles are brought together by the sides of the tube, while the anterior ends of the handles are separated. As the disturbance disappears, the palettes seem dislodged by the ventral retractors, and retraction seems to be completed by the long muscles attached to the ends of the handles. At the same time, by the action of the adductor of the palettes, their paddles are separated, so as to permit the extension of the siphons by an inflow of blood.

From this description, it is seen that the end of the tube of *Teredo* is homologous with the pallial sinus of typical Lamellibranchs. The same siphonal muscles are present as in other forms, while the muscles of the palettes are peculiar to the "Ship-worms".

f. The Respiratory System.

The gills of *Teredo* are perhaps more highly specialized than those of any other type of Lamellibranch. For, besides possessing a membranous, non-perforate portion which reminds one of the gill structure in the Septibranchia, they are otherwise sharply marked off from those of forms nearly related to the "Ship-worms".

The Development and General Structure of the Gills.- The embryonic development of the gills of *Teredo* has been observed by Hatschek (6) in the viviparous larva of the unidentified species studied by him. Here the rudimentary gill of either side is a fold, in which perforations appear in succession, new ones being added posterior to those already formed. In the newly-attached larva, the gills have advanced but little beyond the stage described by Hatschek. On either side there are two slits and the rudiment of a third. However, the slits have so increased in size as to occupy most of the space on the upper sides of the foot, and the gill-fold has fused to the sides of the foot by its ventral edge. In this way, the gill-slits

come to separate bars or filaments attached at both ends (fig. 25). And as the fold, when it appears, is attached at the point of insertion of the mantle on the sides of the body, and the ventral edge fuses with the upper part of the foot the gill-bars or filaments lie almost horizontally in the mantle chamber.

This mode of formation of gill-slits in a fold which fuses continuously, at first with the sides of the body and visceral mass (fig.3) and later, with its fellow of the opposite side as well (fig.6) is kept up during life. However, beginning with stages still less than 1 mm. long, the process is modified as follows:- In specimens less than 1 mm. long (fig. 3) the gill of either side consists of a membrane with a series of gill slits which decrease in size from before backwards. When, however, there are about fifteen slits in the series, a perforation in the gill-fold or membrane appears opposite and internal to the tenth (usually, rarely ninth or eleventh) slit of the first series. New ones are added in succession posterior to it, so that a second series of slits comes to be formed internal to the first (fig. 6). At the posterior end the internal always slightly behind the external in its development. As shown in fig. 6, there are no slits in the in-

ternal series internal to the ten first formed in the external, and none ever appear.

The gill-fold and gill in the young *Teredo* represent the internal half of the Molluscan ctenidium. From the resemblance of the mode of development to that in *Cyclas* (Ziegler) and *Mytilus* (Lacaze-Duthiers), it is seen that the slits of the first formed series separate the descending limbs of the Lamellibranch gill filaments; and that the second series separate the ascending limbs. The anterior ten filaments, then, never develop the ascending limbs. Likewise, the other half of the ctenidium is never developed in *Teredo*, contrary to the belief of Deshayes and Quatrefages, who believed the whole ctenidium, or "pair" of gills to be present on either side of the body.

The term "gill-fold" I have used to designate the posterior end or growing point of the gill, and "gill-filaments", the elements that are formed from it. However, in later stages, soon after that shown in fig. 3, the growing point forms a more or less cylindrical hollow tube filled by a blood space, which fuses continuously on the midline with its fellow of the opposite side, and dorsally over a wide area (between the two points indicated in fig. 37) with the mantle. In this way the spiracular

cavity is separated from the rest of the mantle cavity. Meanwhile, the free portion of the growing point has become angular, and at the sides of the angle the two series of perforations are formed progressively (fig. 6), the external always slightly in advance of the internal. The corresponding slits of the two series push in (in the direction of the lower arrows in fig. 37) till they meet each other and till they push through to the epibranchial cavity. These inpushings divide the original blood space of the growing point into narrow spaces separated from each other except at two points, the openings into the afferent and efferent branchial veins. The median portion of the original blood space remains undivided as the afferent vein, and by the disappearance of the middle part of the walls of the two growing points as they fuse together, the afferent veins of the two sides unite to form the large afferent branchial vein. The undivided dorsal portion persists as the efferent branchial vein on either side. The walls of adjacent slits are connected together by numerous connective-tissue cells (fig. 38), so as to form the gill laminae, the name given to them by Quatrefores, and more appropriate for the gill elements in *Terebr*

which (except the anterior ten) do not form filaments. From the mode of formation it is seen that there is a large flat blood space in each lamina, and that there is a free flow of blood through the lamina (in the direction of the arrows fig. 37) between the afferent and efferent branchial veins.

In a young *Teredo* a half centimeter in length (somewhat later than the stage represented in fig. 6), there is on either side a continuous series of seventy-five or more gill filaments (filaments and laminae), stretching from the mouth region, around the sides of the body, and posterior to the visceral mass. Soon afterwards the "filament" between the tenth and eleventh (usually) gill-slits broadens from before backwards. This growth increases till, in the adult, the anterior ten filaments (it may rarely be nine or eleven) are separated from the rest of the gill by ten cm. or more, in large specimens. However, they retain the structure and, doubtless, the function of gill elements, though in the adult, they form a series of plications on the sides of the "head" (fig.9).

In *Teredo*, the epibranchial cavity forms a long canal posteriorly (figs. 10,33,34) but is divided anterior-

ly where the gills of the two sides diverge from each other. As the anterior ten filaments become separated from the rest of the gill, the epibranchial cavity remains as a long, very narrow canal (cp. ca. figs. 28-31) which lies in the mantle on either side external to the afferent branchial vein, and adjacent to the groove described below.

The two limbs of a gill lamina (fig.37) form almost a right angle with each other. At the angle there is a ciliated groove (figs. 32,34, 37) which expands the full length of the gill in young specimens (fig.6), and in adults, in addition, connects the anterior ten filaments with the rest of the gill (figs. 9,28-31). In the adult, the connecting part of the groove, then, is really a part of the gill and is homologous with the groove of one filament in other parts of the gill. The minute structure of the groove is as follows:- The lining cells are in the main strongly ciliated and columnar (fig.44), but there are distributed among them numerous mucous gland cells. The internal surface of the mantle opposite the edge of the gill, also forms a groove lined by strongly ciliated cells with gland cells among them, and this with the groove of the gill forms a sort of tube which conveys food to the

mouth.

The Minute Structure of the Gills. - It has been seen that, by their mode of formation, the "intra-filamentar union" between the two limbs of a lamina is so complete, that blood may flow freely through the lamina from the afferent to the efferent branchial vein. The "inter-filamentar" connection, between adjacent laminae is also very complete, but serves only for support and not for the full interchange of blood. The general plan of the inter-laminar connections is shown in fig. 39, which is a tangential section of a gill almost in the line of the letters if.j. in fig. 38. It is seen that the points of union in adjacent laminae are arranged in regular rows. At each point, the supporting rod (s.r. fig.40) projects through a perforation, so as to bind together adjacent laminae. Attached to adjacent rods are fiber-like cells which are apparently muscular and contractile.

The minute structure of the edges of a lamina is similar to that of the filaments in forms like *Mytilus*, though the various types of cells are more sharply marked off from each other. At either side there are two rows of

large "lateral cells" (l.c. fig.40), bearing long dense cilia. External to these are small non-ciliated gland cells, and at the angles, the small, flattened "latero-frontal" cells (l.f.c. fig.40), with a single row of stiff cilia. The outer edge of the lamina is occupied by numerous small "frontal-cells" (f.c.) which bear numerous weaker cilia. The two broad sides of the lamina are composed of very flat cells without cell outlines or regular arrangement, and are connected together by numerous connective tissue cells which penetrate the blood space of the lamina (b.S. figs. 38,40). In their minute structure (fig.41) the anterior ten filaments are essentially like the rest of the gill, except that the "frontal cells" are more numerous, and the middle ones bear no cilia. The first filament is only a half filament, indicating that the filaments are formed by perforations in a gill membrane, and not by the latter precocious fusion of gill filaments. The long epibranchial canal is sparsely ciliated, and it seems that the function of the anterior ten filaments is to get rid of superfluous water in the anterior end of the burrow.

Glands of Deshayes. - Closely associated with the gills of the adult is a pair of very complicated structures which, so far as known, are peculiar to *Teredo*, and which constitute one of the most important features which distinguish the "Ship-worms" from other types of Lamelli-branchs. In honor of the observer who first described them, I have called them the glands of Deshayes. Though he pointed them out, they have never been fully described as to character, structure and relations.

Deshayes observed a peculiar structure in the umbo-nal region on either side of the shell cavity. He described it as of glandular nature, and supposed its function to be the secretion of a fluid to soften wood in the formation of the burrow. In the gill laminae he described peculiar modifications of the tissues, which he supposed to be mucous glands, and to serve for the nutrition of the viviparous embryos of *Teredo*. He also described a third structure, as invading a part of the walls of the afferent branchial vein, and of unknown function. These three glands described by Deshayes are parts of one and the same structure which is present, in different degree of development, in all of the three species I have studied. In all three the part in the gill is well developed. In *T.*

norvegica, the umbonal part is so large as to occupy a considerable part of the umbonal region of the shell cavity; in *X. fimbriata* it is small, and in *T. navalis*, apparently rudimentary. In his studies of the pericardial glands in Lamellibranchs, Grobben sought in *Teredo* for the gland described by Deshayes in the umbonal region, thinking it might represent a part of the pericardial gland of other forms which possess this organ. He failed to find it and supposed it to be absent. However, though he apparently had none of the forms with which I have worked, I think it was doubtless present in his species.

In the larva this peculiar structure is present on either side in front of the cerebral ganglion, though in a much simplified form (g.D. fig.2). It is vesicular and filled with spherical cells of apparently nucous nature. A duct leads to the exterior, opening at the side of the mouth, on the ventral side of the velum.

The structure of subsequent stages of the gland will be best understood by first describing that part in the gill. A glance at fig. 38 will show that the modified portion contains elements of two very different types of structure. Their distribution and relations are best shown in fig.37, which represents a lamina from the gill of

T. navalis. This figure also shows the distribution of the gland in the branchial vein, and that this portion is of the same nature as that lying in the lamina adjacent to it. Still farther from the vein, is the second type of structure. Ramifying in all directions from the latter are dendritic processes, which penetrate the epithelial walls of the lamina. These ramified portions are the primary structures, and the other two are derived from them. The structure of the dendritic portion is shown in figs. 47, 48, which were drawn under a magnification of 1900 diameter. The processes seem devoid of any membrane. The contents consist of very minute filamentous structures arranged lengthwise in the direction of the process. Lying in the mass thus formed are nuclei which vary in number and position. The middle one in fig. 48 indicates that they may change position, and that the whole structure forms a syncytium. The enlarged portions of the processes shown in fig. 37, became surrounded by an epithelial covering, apparently derived from the lining cells of the lamina. This stage is represented in figs. 46 and 47. The minute filamentous structures have taken on a more irregular arrangement, and lying within the mass are spher-

ical cells of varying appearance. While some (fig. 45) are coarsely granular, others are almost homogenous. The nuclei lie to one side of the cells.

The other type of structure (figs. 50-52) I am confident though not perfectly sure, is also derived from the dendritic processes, along with a modification of the surrounding epithelium. The developed structure is of remarkable appearance (fig. 52). The base is composed of modified epithelium cells of the wall of the lamina. The nuclei stain lightly and lie in a granular protoplasm, from which deeply staining rods project into the blood-space, but from which they are separated by a membrane formed of very flat cells. The development of this structure seems to be as follows: When the dendritic processes penetrate among the epithelial cells (fig. 49), the filaments are arranged lengthwise; soon they take on a vertical position (fig. 50) enlarge, and become covered by the cap-like membrane (figs. 50-52). If this derivation be the correct one, then the rods in fig. 52 have been formed by the enlargement of the filaments of the dendritic structures. In the lamina the rods project into the blood-space; in the afferent branchial vein, away from the

blood space. Why the difference, I do not know.

The development of the gland of the adult, so far as I can determine, is as follows:- When the small *Teredo* have been in the wood for a day or so, the gland of the larva sends out processes which invade the surrounding ectodermal tissues (the mantle, sides of the body). As the side of the body becomes enlarged, it fuses with the dorsal sides of the gill filaments (fig. 27). From the first there is close association between the gland and the gill. As the latter grows, the filaments become invaded by the gland; and as the anterior ten filaments become separated from the rest of the gill, the two parts of the gland remain connected together by a long, narrow duct which accompanies the epibranchial canal and lies in the afferent branchial vein (figs. 28-32). With the separation of the two parts of the gill, the intervening part of the gland disappears in *X. fimbriata* and *T. navalis*, but persists in *T. norvegica*. As the gland enters the gill lamina, it remains connected by a small duct with the main duct, and sends the granular cells into the latter. The main duct may become gorged with granular cells (fig. 47). However, in most cases there are few cells in it, and I am inclined

to regard it (at least in *X. fimbriata*) as degenerate. Likewise, I am inclined to regard the formation of the spherical cells, in the one part, as not the chief function of this part of the gland. The origin and fate of the cells I have not been able to determine. Their contents suggest that they may be modified mucous gland cells.

What the special function of this remarkable structure is I am not able to even guess. The rudimentary character of the anterior part in the "head" of *T. navalis* indicates that it cannot be the formation of a secretion to soften wood. Its development in the gill, in small as well as large individuals, in male and female, and in forms that do not retain the eggs in the gills, proves that this part cannot be for the nutrition of viviparous embryos. The close connection with the gill indicates, it seems to me, that its function is probably the elaboration of some internal secretion for whose formation the presence of both blood and water is necessary.

g. The Circulatory System.

The circulatory system of the "Ship-worms" is peculiar in relation to the peculiar form of the body. The growth of the visceral mass ventrally at first, and afterwards its great elongation posteriorly along with the elongation of the rest of the body accounts for the changes that have taken place. Doubtless the ancestors of *Teredo* were Lamellibranchs with typical circulation, in which on either side in the pericardial cavity lay an auricle latent to, and emptying into, the median ventricle which surrounded the intestine.. From the ventricle the anterior aorta passed forward above the intestine and the posterior aorta backward below the intestine. In *Teredo*, the pericardial space, with its contained parts, has come to lie on the morphologically ventral side of the intestine, and the relations of the various parts of the circulatory system to each other have been radically changed.

The youngest stage of the circulatory system I have observed in detail is in specimens 2 mm. long. Here the heart consists of two almost separate halves (fig. 52). On either side a more or less spherical auricle (an.) lies lateral and slightly ventral to, and leads into, a more or

less spherical ventricle (ve.) Either ventricle sends a very narrow, vessel-like portion towards the mid-line where the two sides unite. In this middle portion there are two semilunar valves (fig. 55) on the dorsal and ventral sides, and from this point two vessels emerge. One runs anteriorly, and bending around the posterior adductor muscle, runs posteriorly in the mantle. At this stage, the visceral mass has projected but little posteriorly (fig. 6), and the second vessel from the heart, somewhat smaller than the other, runs ventrally into the visceral mass. These structures are shown in section in fig. 54, which is a longitudinal section through the median part of the ventricles and aortae in a specimen 4 mm. long.

In the stage in which the heart is developing, the stomach and caecum already occupy most of the visceral mass, and the gills are wide apart. This may account for the wide separation of the two halves of the heart. In development posteriorly, the gills advance ahead of the other structures and, accompanying them the two sides of the heart are drawn backwards so as to lie side by side. In the adult (fig. 54) the ventricles (ve.) have fused on the midline, except at the posterior end, where the two

sides still project as somewhat hemispherical masses. However, internally the lumen remains divided (fig. 1) through half of the extent of the ventricles. At the anterior end, the ventricle has the shape of an elongated cone. The two auricles accompany the gills in the posterior development of the latter and come to lie side by side like two large vessels, in the posterior half of the pericardial cavity. Each projects into the ventricle on its own side and valves separate the cavities of the auricles from that of the ventricle (fig. 54).

The pericardial cavity of the "Ship-worms" (figs. 10, 31, 32) lies on the apparent dorsal side of the visceral mass. It is very large, extending from the posterior adductor to the visceral ganglion. In *Xylotrya fimbriata*, it narrows in front to form a canal which projects beyond the wider part to the posterior adductor muscle. About two-thirds of the distance from the visceral ganglion to the posterior adductor (fig. 10) the anterior end of the ventricle dips down through the pericardium, into the visceral mass. This point is the end of the ventricle and the beginning of the aortae, the end of the ventricle being marked off by two semilunar valves which project

forwards on its dorsal and ventral sides (val. fig. 56). From the end of the ventricle two vessels are given off. The larger (av. r. figs. 10, 56) runs forwards (figs. 29-30) in the visceral mass, and passes ventral to and in front of the posterior adductor, to bend over the latter and enter the mantle as the large dorsal or posterior pallial artery. This runs as a single vessel in *Xylotrya* at the right side of the anal canal and epibranchial cavity (figs. 28-34, d.a.) to the posterior end of the body, where it divides into the two paired arteries of the siphons. This aorta I have just described is the morphological posterior aorta, though its course at first is anteriorly. The second aorta leaving the ventricle runs posteriorly in the visceral mass and is the morphological anterior aorta.

The venous system consists of three important parts. Blood from the viscera and anterior part of the body is gathered into a system of afferent branchial veins consisting anteriorly of large paired vessels (G.a. figs. 29-31), which in the region of the visceral ganglion unite to form the very large afferent branchial vein which runs between the fused gills (figs. 10, 32-34). Passing from this vein through the gill lamellae, it enters the large

paired different branchial veins which enter the auricles. Blood from the posterior part of the body is gathered into an afferent renal vein (a.r.v. figs. 33,34) which runs forward and enters the pericardial spaces, at the posterior ends of the kidneys.

The description I have just given applies to *X. fimbriata* and *T. navalis*. In *T. norvegica*, while the relations are somewhat different, the homologies remain the same. In this species, the principal part of the visceral mass has remained more anteriorly and the posterior part of the body is longer in proportion. In following the gills, the heart has become much more elongated, and this elongation has taken place in the aorta-like structure which runs forward from the more thickened portion of the ventricle. In this species, the pericardial cavity extends much further forwards than in *X. fimbriata*, passing under and anterior to the posterior adductor muscle as a long canal, to end under the oesophagus. In it, the ventricle runs to the anterior side of the posterior adductor, to dip into the visceral mass. Valves mark the end of the very long ventricle, from which two vessels pass forwards. The larger, after giving off branches in its

course, turns around the adductor, and divides into paired pallial arteries which supply the posterior part of the body. This is the posterior aorta. The other, the anterior aorta also runs forwards a short distance, but soon breaks up in the visceral mass.

I have gone into details in describing the aortae, because the posterior aorta is described as fused with the anterior in *Teredo*. This observation was first made by Grobben (5), who described as aorta a part of the ventricle which is distinctly muscular and contractile. The part that should have been described as aorta he has not figured at all. Menegaux has also maintained that the two aortae are fused (11). Unfortunately, neither of these workers names the species with which he worked, but their descriptions of other parts are so faulty as to indicate that there is little doubt that they have been in error in this regard.

h. The Alimentary Canal.

In adaptation to their burrowing mode of life, the alimentary canal of all the Pholadacea has become more highly specialized, perhaps, than in any other type of Lamellibranch. This specialization is carried farthest in the "Ship-worms".

Most of the parts of the alimentary canal of the adult are already present in the newly-attached larva, though their relations to each other and their relative development are very different. The general plan is shown in fig. 2, which represents a larva from the right side with the shell, mantle and gills removed. A long ciliated oesophagus (figs. 2, 24, oe.) leads into a rather small stomach, from which project on either side the two large, simple liver lobules, composed of large, coarsely granular, pigmented, non-ciliated cells (figs. 2, 25). The intestine leaves the right side of the stomach, (figs. 2, 26) and after forming a single loop passes over the posterior adductor as the rectum. Just posterior to the intestinal opening is a small hemispherical diverticulum of the stomach, the caecum (ce. figs. 2, 25, 26) composed of densely granular, non-ciliated cells. The posterior, ventral

part of the stomach is occupied by the opening of a large, conical diverticulum which is median in position, the sheath of the crystalline style (S.S. figs. 2, 4). Its walls are composed of the large, coarsely granular, densely ciliated cells characteristic of this structure, except at the blind end, where the cells are smaller, more finely granular and non-ciliated. (fig. 24).

The alimentary canal of the larva is interesting because of the advanced development of some parts and the retarded development of others. The liver has advanced but little in form beyond a stage reached two or three days after hatching. On the other hand, the caecum of the stomach, which is peculiar to the members of the Pholadarea, is already present as a rudiment, although it is not to become functional till after the adoption of the life in the wood.

As the larva develops into the "Ship-worm", the size and relations of the parts of the alimentary canal change greatly. The oesophagus becomes, in the adult, very short in comparison with other parts (fig. 10). The stomach elongates posteriorly more and more (figs. 4, 7, .) till in the adult it projects far beyond the posterior adductor and forms a long cylindrical tube (fig. 10). As is well

known, the wood rated away in boring, is ingested and stored in the caecum of the stomach. Even before the ingestion of the wood begins, the caecum projects into the foot as a large hollow vesicle, lined by clear, ciliated cells. But, as soon as wood is ingested, it enlarges rapidly and soon forms the largest part of the alimentary canal (figs. 4,7,10 (e.)). With its increase in size, it comes to leave the posterior end of the stomach, and crowds the sheath of the crystalline style to the left side (figs. 4,7,10). In young specimens, the caecum occupies almost the whole mass of the foot, and its blind end points forwards (figs. 4,7). As the visceral mass elongates, the caecum is gradually drawn backwards, till in the adult, it forms a very long cylindrical tube, stretching to the posterior end of the visceral mass (fig.10 (e.)) In "Ship-worms" that are boring and growing, the caecum is always completely filled with ingested particles of wood. The scarcity of diatoms and other food materials seems to indicate that in the "Ship-worm", boring and ingestion of wood, and ingestion of food alternate, and that, when feeding, the food is guided into the intestine; and when boring, into the caecum. The caecum, then, is a long,

blind tube, opening only at its anterior end into the stomach. Internally it is lined by a ciliated mucous membrane, which is folded like a typhlosole (figs. 32, 33), but the fold seems of independent origin, and not at all homologous with the fold in the intestine. The long retention of woody particles in the caecum, along with the greatly increased absorbent surface of the latter, indicates that the wood is in part digested and serves as food.

In elongating posteriorly the caecum pushes the intestine ahead of it, so that the latter always forms a very long straight loop around the former. The intestine, along with the great development of the caecum, and the greater development of the liver on the right side, in the adult leaves the stomach slightly to the left of the midline, near the posterior end (fig. 10). Bending forwards, it forms a single short loop and then passes backwards to form the loop around the caecum. Then passing dorsal to the stomach it bends over the posterior adductor as the rectum (r) which projects slightly into the anal canal. Throughout its whole extent the intestine possesses a typhlosole, but slightly developed, except in that part next to the stomach. Here the typhlosole is so greatly

developed as to form several coils (fig.29) which cause the intestine in this region to be greatly enlarged (fig. 10). The intestine of *M. finbriata* is very much shorter than in other "Ship-worms". The shortening of the intestine is doubtless connected with the greatly increased absorbent surface of the coiled typhlosole. In most "Ship-worms" the intestine forms several coils before it passes around the caecum and in such forms there is no greatly coiled typhlosole.

In *Teredo*, as in *Pholas*, there is a second small, quill-shaped caecum of the stomach on the dorsal side to the left, under the posterior adductor (see figs. 7,10, 23). It is lined by columnar, ciliated cells and generally contains particles of sand. It is small and seems degenerate, but it may have some function at the present time. Pelsener has observed an apparently homologous structure in *Mucula*, where it is said to secrete a small style.

The sheath of the crystalline style, present on the midline of the larva, comes to open from the left side of the stomach near the anterior end of the latter (U.S. figs. 7,10), and hangs towards the right side. Its blind end

forms a vermiform tube, which is very different from the rest of the sheath. The latter has its walls composed of large coarsely granular, cells, which bear very heavy, dense cilia (fig. 57, A.). The tubular portion, on the other hand, has its walls composed of elongated, densely granular and deeply staining, non-ciliated cells. In adults, the walls of the tube may become very thin (fig. 57 B.) in parts. What the function of this tubular portion is I am not able to state, though it is perhaps the secretion of some constituent of the style. Barrois (1) has figured a pair of diverticula at the ends of the sheath of *Pholas dactylus*, lined by cells similar to those of the rest of the sheath. On examining sections of apparently specimens of the same species, I find a tube, as in *Teredo*, lined by cells of the same character as in the latter, so that I am inclined to believe that Barrois' description and figures are faulty.

The liver, composed of a simple spherical lobule on either side of the stomach in the larva, soon divides into several lobules on either side (l. figs. 4,7). As growth takes place, the duct of the right half of the liver divides (in specimens 4-5 mm. long), and as the "Ship-

worm" elongates, the posterior part of the right half of the liver passes backwards, so that in the adult, its duct opens into the posterior end of the stomach. The anterior and posterior portions of the liver are completely separated from each other, forming separate liver masses (fig. 10). The anterior remains in the foot, and sends its duct to open into the external anterior portion of the stomach. There seems little doubt that it was this part which Frey and Lenckart observed and described as the salivary glands peculiar to *Teredo*. The posterior part of the liver is the larger of the two, and opens by a very large duct into the ventral part of the stomach. It is differentiated into two portions, which in structure and apparently in function, are quite distinct from each other, though they open into the stomach by the same duct. The more elongated, slightly larger portion (fig. 30) lies on the right side, and in structure is like the anterior liver mass of *Teredo* and the whole liver in other forms of Lamellibranchs. The second portion (fig. 30) lying more on the left side, is different in appearance. Its lobules are larger, with larger lumens and thinner walls, which are composed of flattened less glandular cells. The presence of large

quantities of woody particles in these latter, thin-walled lobules suggests that this portion of the liver may be specialized for the digestion of cellulose, and this view is strengthened by the long retention of woody materials in the caecum. This portion of the liver is adjacent to the opening of the caecum, and it may be that it secretes a ferment for cellulose digestion which is continued in the caecum. As has been pointed out already, the latter by its structure seems adapted to absorption on a large scale.

i. The Nervous System.

The nervous system of "Ship-worms" I have studied in the larval and subsequent stages of *Xylotrya fimbriata*, and in the adult of *T. navalis* and *T. norvegica*. While my description applies especially to the first of these, the others are in such close agreement, that we seem justified in believing that there is great uniformity in this regard in all of the species of the Teredinidae, and that the descriptions heretofore given have been erroneous.

The Nervous System of the Larva. - In the larva the principal elements of the adult are present. However, in their relations to each other, their embryonic development is not complete; and in their relation to other structures great changes take place along with the change in the general organization. The general plan is shown in figs. 2 and 59, the latter representing a dorsal view of the nervous system of a larva just attached. In front of and on the sides of the mouth are the two cerebral ganglia, (c) separated by a very short commissure, and each sending a

connective to the pedal ganglion (1) of the same side. At the side of the cerebral are the pleural ganglia, distinctly separated from them, and sending connectives posteriorly to the visceral ganglia. I think there is also a pleuro-pedal connective at this stage, but this I am not able to state positively. The pedal ganglia at this stage are as completely fused as in the adult, and lie just posterior to the beginning of the oesophagus (fig. 24). Lying immediately in front of the posterior adductor muscle (figs. 2, 24, 26), the visceral ganglia form a long cylinder enlarged at both ends. The commissure here contains ganglion cells. The two sides rapidly become more closely fused and in the early stage represented in fig. 4, the concentration is almost as great as in the adult. Each visceral ganglion of the larva gives off a respiratory nerve which bears a respiratory ganglion still far apart from the visceral. While the visceral ganglia are becoming more closely fused, the commissures between the cerebral and pleural ganglia are becoming obliterated. These ganglia persist as separate masses in the young "Ship-form" of three or four days (fig. 4), but soon afterwards fuse completely, though sections of latter stages still

indicate by their structure the double origin of the so-called cerebral ganglia.

While these concentrations of the visceral ganglia with each other and of the pleural with the cerebral have been taking place, the cerebral commissure is constantly elongating, along with the growth of the oesophagus, so that in the adult, the cerebral ganglia are separated from each other by a long commissure.

The Nervous System of the Adult. - Along with the great change in the general relations of the various systems that have taken place from the "Ship-worm" larva to the adult, the nervous system has changed, principally in the changed position of the visceral ganglia, which lose their position in front of the posterior adductor, and come to lie much posterior to it. However, the same three pairs of ganglia are present in the "Ship-worms" as in other types of Lamellibranchs. The general arrangement is shown in fig. 60. Lying almost at the sides of the mouth are the two cerebral ganglia (c. figs. 10, 60), well developed

and separated from each other by a long commissure (c.c.), which is composed only of nerve fibres. From near the outer end of either, a single large pallial nerve passes, to be distributed to the anterior part of the mantle which underlies the shell, and forms the cephalic hood. From near the inner ends of the ganglia large connectives pass around the sides of the mouth to the pedal ganglia (p); and, from the posterior outer ends, the cerebro-visceral connectives pass posteriorly to the visceral ganglia. The pedal ganglia give off several pairs of large nerves which innervate the foot.

The Visceral Ganglia. - The two visceral (v.fig. 10,60) ganglia of the larva fuse into the single mass which lies very far posteriorly in the adult (v.fig.10). After leaving the cerebro-pleural ganglia, their connectives with the visceral pass along the sides of the "head" under the anterior gill filaments; but, posterior to the large adductor muscle, they take up a more median position, among the tissues of the liver and genital organs. In front of the visceral ganglia they come to lie close together, internal

to the large, duct-like portions of the genital organs. But before entering the visceral ganglia, they pass dorsal to a small "anterior ganglion" which lies just in front of the latter. In passing it, they lose a small amount of nerve fibres (fig. 63), which are lost in it. Then the connectives enter the visceral ganglia, but little diminished in size. This anterior ganglion was first described by Pelseneer (13) for the "Ship-worms" and seems peculiar to them and their allies. It is a small ganglionic mass lying distinctly in front of the visceral in well preserved specimens, and from the fibres crossing between the sides it seems composed of two halves, quite completely fused together. As has been stated, the connectives in passing, send fibres ventrally into it, to be completely lost in it. From this ganglion several pairs of nerves are given off which innervate the kidneys and other viscera, the genital papillae and the oesophradium, at least in part (fig. 60). From the anterior end, a pair passes forwards to supply the genital organs and perhaps other viscera. From the middle of the ganglion a pair passes laterally to innervate the genital papillae and the kidneys (fig. 63). Leaving the posterior lateral angles of the ganglion, the

largest pair of nerves pass backwards under the visceral, and divide each into two parts. The one, somewhat larger than the other, passes dorsally to enter, and be lost in the mass of the visceral ganglia. The other passes laterally to innervate the osphradium.

The visceral ganglia proper of the adult (figs. 10, 60), along with the greater development of the posterior part of the body innervated by them, have attained greater comparative size than the cerebral and pedal. They form a somewhat three lobed mass, in which the larger, central, part consists of the completely fused visceral ganglia of the larva, while the lobe on either side consists of the respiratory ganglia which have come to lie adjacent to the visceral proper.

From the visceral ganglia several pairs of nerves are given off, whose connection with the visceral is through the lateral masses (fig. 60). Passing forwards on either side are two small nerves (figs. 60,1,2) which accompany the kidneys and anal canal, which innervate the posterior adductor and the anterior part of the mantle. Given off slightly posterior to them, a large nerve (3) goes directly to the middle part of the mantle. Posterior-

ly, a pair of large pallial nerves (p.n. figs. 23-5, 60) passes backwards to innervate the posterior part of the mantle, including the siphons and the muscles of the palottes. The branchial nerves (b.u.) pass laterally, closely associated with the osphradium, and then innervate the gills.

This description of the nervous system differs essentially from that of Quatrefages (15) which has heretofore been accepted. He thought the two cerebral ganglia closely fused and the pedal rudimentary and separate. I have no doubt that he mistook the pedal ganglia for the cerebrals; his figures show this. But what he observed and figured as the two very small pedal ganglia I do not know. It has been seen that while they are not so large as in forms with a large foot, they are not at all rudimentary.

Otolith. - The larva leads an active locomotor life, and some means for distinguishing the position of its possessor is very essential. But the adult "Ship-worm" may assume any position, and the otoliths become useless and degenerate. After attachment, they soon cease to grow, and

in specimens two or three mm. long, their function seems lost, though they persist as small masses of cells in the adult.

Sense-Organ of the Genital Papilla. - One of the pairs of nerves of the anterior ganglion has been described as going to the kidneys and genital papillae. Situated just at the junction of the ectodermal genital duct, with the sexual organ there is an organ which by its structure seems to be for special sensation. The nerve to it (figs. 63, 64) after a very short course is distributed to sensory cells which lie adjacent to the epithelial lining of the genital duct. The sensory cells are long spindle-shaped, and send their peripheral ends to terminate among the epithelial cells lining the genital duct. Their central ends I have not traced into the nerve, but it seems justifiable to suppose that this is their connection. What the function of this organ is I cannot state. While the figures apparently show it some distance from the exterior, it should be remembered that in "Ship-worms" 30 cm. long, the sexual duct is less than a half mm. long, and that the

sense organ is really very near to and for purposes of sensation, practically at the surface.

The Osphradia. - These Molluscan organs of special sense form large masses of complex tissues at either side of the visceral ganglion.(fig.60). Their general shape is elliptical and they are in close association with the branchial nerves. Each organ (fig.61) is composed of two parts. At the ventral (outer) surface, there is a part of the body epithelium, which in this region is specially differentiated from the surrounding cells. While the epithelium of the epibranchial cavity is ciliated, the osphradial epithelium is quite devoid of cilia. Besides, the cells composing the osphradial epithelium seem to have quite lost their cell-walls, so that the spherical nuclei lie in a common mass of protoplasm. The outer surface of the epithelial layer is covered by a very delicate membrane, and at its internal surface there is a stouter basal membrane. Underlying the surface epithelium is a mass of nervous elements, composed of both cells and nerve fibres. The cells, however, are sensory and stain somewhat differently from the ordinary ganglion cells. These sensory

cells are of two kinds, both spindle-shaped and sending their peripheral ends through the basement membrane of the overlying epithelium, to break up into brush-like terminations just inside the delicate outer membrane of the epithelium. These structures are shown in figs. 61 and 62. In fig. 61, the two types of cells are shown, the larger one to the left representing the type much less numerous than the other, staining differently from them and penetrating the osphradial mass to terminate centrally differently from the smaller, more numerous cells. The internal or central connections I have not been able to determine, but this much it seems justifiable to state. The osphradial nerve from the anterior ganglion becomes so closely associated with the respiratory nerve, that it cannot be stated that it alone supplies the osphradium. Also, the large sensory cells penetrate through the osphradial mass, and especially it cannot be stated that their connection is with the osphradial nerve.

These structures I have described in detail for two reasons. In the first place, the epithelium of the osphradium is usually described as consisting of columnar cells, which form the sensory part of the structure. This I have

it and to consist of a layer in which cell outlines are not distinguishable, and in which the spherical nuclei lie as in syncytium. The real sensory cells are the spindle-shaped cells lying in the deeper part of the osphradium.

In the second place, Pelseneer (10) has described the osphradium in *Teredo* and *Pholas* as innervated by a nerve from the anterior ganglion, and the latter as connected with the cerebral ganglia through the connectives. From this he concludes that the osphradia, as well as the other organs of special sense, are innervated from the cerebral ganglia. The organization of the nervous system in *Teredo*, it seems to me, lends no evidence whatever to this view. The nerve fibres received from the connectives by the anterior ganglion are quite lost in the latter and cannot be traced into any of the nerves which leave it. Moreover, the anterior ganglion may with much more reason be said to be connected with the visceral ganglion, for the branch of the so-called osphradial nerve from it to the latter, is much larger than the nervous elements received by it from the cerebro-visceral connectives. Pelseneer seems not to have seen the other nerves that leave the anterior ganglion. With as much reason it might be

said that the structures they supply also are innervated from the cerebral ganglia. Nerve fibres, it may be, pass from these structures through the anterior ganglion to the cerebral, but that the latter are the only centres in which reflexes may be established seems not in accordance with the structure of the nervous system in *Teredo*. It seems more plausible to regard the anterior ganglion as a part of the visceral which has been separated from the latter. It receives a part of the cerebro-visceral connective, and gives off some of the nerves that formerly were given off by the visceral.

From a theoretical standpoint, too, one would expect elongated forms like *Teredo* and *Pholas* to have a more direct connection between the osphradia and the reflex centres. If the osphradia test the character of the water flowing over the gills, then it is difficult to believe that in a large "Ship-worm" the nerve impulse should travel from them to the cerebral ganglion and back again through the visceral ganglia to the pallial nerves before the siphons can be contracted and the inhalent current stopped. This would necessitate a course of almost two metres in very large specimens. The more direct connec-

tion through the visceral ganglion is the one it seems reasonable to expect.

j. The Kidneys.

The kidneys (organs of Bojanus, nephridia) of *Teredo* were observed, apparently, by Deshayes, but mistaken for veins. Quatrefages also observed them but gave no adequate description. Pelseneer (14) has noted the position and relations of the openings of the two ducts.

In the adult "Ship-worm" the paired kidneys lie on the dorsal side of the large pericardial cavity and ventral to the anal canal, extending the long distance between the posterior adductor muscle and the visceral ganglion. Each kidney consists of what may be termed the body, which lies around the posterior face of the posterior adductor muscle (k., fig. 10); and two very long ducts, one of which puts the body in communication with the pericardial cavity, while the other leads to the exterior. The

body is a massive, much pouches structure in which the lining secretory epithelium is vacuolated and in part ciliated. From the body the very long, narrow, cylindrical afferent duct passes posteriorly (ka., figs. 29-31) near the midline. Just in front of the visceral ganglion it enlarges, becomes convoluted internally, diverges from its fellow of the opposite side (k.a fig. 66) and dips under the end of the efferent duct (fig.65) to open into the posterior angles of the pericardial cavity (fig.32) by a large funnel-shaped opening. The lining cells of the afferent duct are not vacuolated and apparently not excretory; and, are not ciliated except in the enlarged, funnel-shaped portion in which they bear strikingly long, dense cilia (fig. 64).

The efferent duct, leading from the body of the kidney to the exterior, is also a cylindrical tube, of much larger diameter than the afferent duct. It runs with the latter near the mid-line (k.e., figs. 10,29-31) and in front of the visceral ganglia, after diverging slightly from its fellow of the opposite side (fig. 66), it crosses dorsal to the end of the afferent duct. Then it passes to ventrally and posteriorly (figs. 35, 36) to open near the

midline into the epibranchial cavity, under the visceral ganglion. The efferent duct is lined by columnar, vacuolated and apparently secretory cells, which are not ciliated except at the anterior end, and also near the external opening.

Venous blood from the posterior end of the body returns by an efferent renal vein (figs. 33,34, a.r.v.) which runs in the mantle, and on a level with the posterior ends of the kidney duct, enters the peri-renal blood spaces (figs. 29-31). After bathing the kidneys, it enters the general venous circulation.

Pelseneer, who, it seems, observed only the posterior ends of the kidney ducts, described them as much pouched. In properly prepared specimens of *X. fimbriata*, I find that, while the body of the kidney is much pouched, the ducts form straight cylindrical tubes. Preserved "Ship-worms" are almost always very greatly shrunken, and I am inclined to believe that this fact accounts for Pelseneer's results. Also, contrary to the statements in textbooks (Lang), I find that the two kidneys of *X. fimbriata* do not communicate with each other, as they do in *Thalassidroma* and other forms.

In the larva, the kidneys lie anterior to the posterior adductor muscle, and lateral to the visceral ganglion (figs. 2,26). As the visceral ganglion passes under and posterior to the muscle, the kidneys accompany it (fig. 7). In the early stages each kidney consists of a single loop (fig. 7) of which the branch opening to the exterior is the excretory. As the "Ship-worm" elongates, the chief secretory portion of the kidney remains with the muscle, while the two ducts become very long, and their openings accompany the visceral ganglion.

k. The Reproductive Organs.

The first stage in which I have observed the reproductive organs, is in specimens 2 mm. long, in which there is a mass of germ cells under the visceral ganglion (g.o. fig. 7). As growth takes place, processes grow out from the original organ, till in the adult, the sexual organs occupy a large part of the posterior part of the visceral mass (figs. 10,31-33.). As the sexual products develop,

they are stored in the cavities of the organ and especially of that part first formed (figs. 33, 34, ov.) which serves as a duct for the rest of the organ. The real sexual duct is remarkably short. It is formed as an ectodermal invagination which is already present in specimens 2 mm. long, but which does not break through till sexual maturity.

In the adult *Teredo*, the sexes are separate. However, young specimens (1-4 cm. long) of *T. fimbriata* are very frequently hermaphrodite. As in all such cases the sperms are developed first, it appears as if the species may be propandrous. In the adults, I have observed no external differences between the sexes. However, in the male, there is a remarkable development of mucous gland cells on the dorsal side of the epibranchial cavity; while in the female, they are not unusually developed in this region.

1. Summary.

The result of my work on *Teredo* may be summarized as follows: The larva of *Teredo* is a typical free-swimming marine Lamellibranch larva. The whole velum is suddenly cast off and eaten, soon after the attachment of the larva. After the loss of the velum the young *Teredo* is a typical small bivalve. The loss of the velum in *Teredo* and in *Ostrea* (which I have also observed), indicates that the formation of the palps in Lamellibranchs has no connection with the velum. A byssus apparatus is present in the newly-attached larva. It is functional for but a few hours. The position and relations of the sheath of the crystalline style in the larva indicate that this structure, in the more highly specialized Lamellibranchs, is homologous with the posterior half of the stomach in forms like *Yoldia* and *Nucula*. The pleural ganglion of the larva is separate from the cerebral.

The transformation of the *Teredo* larva into the small "Ship-worm" is so rapid as to amount to a metamorphosis. Almost the whole organization is involved - shell, mantle, foot, alimentary canal. The posterior adductor is the effective agent in forming the burrow, and the shell

is the tool with which it works.

In the "Ship-worms", there is a peculiar gland in the mantle of the posterior part of the body. A system of highly specialized muscles manipulate the palettes and are peculiar to *Teredo*. There is on either side but a half ctenidium. The anterior ten filaments form small plications on the side of the "head", separated from the rest of the gill by a long distance. In close association with the gills is a prominent glandular structure of unknown function. It consists of two types of elements of remarkable character.

Through the elongation of the visceral mass, the positions of the two aortae have been reversed; i.e., the apparent posterior aorta is the real anterior, and the apparent anterior the real posterior. The caecum of the stomach is very large and apparently an important absorbent organ. The blind end of the style sheath is tubular and of very different character from the outer part. In *Xylotrya* the typhlosole of the anterior part of the intestine is remarkably developed.

The nervous system contains the three pairs of ganglia, well developed, as in typical Lamellibranchs. The

pedal ganglia are fused together, the cerebral, separated from each other by a long commissure. The small "anterior ganglion" innervates the kidneys, genital organs, and osphradium in part. On the genital duct is an organ of special sense, of unknown function. The sensory cells of the osphradium lie beneath the surface epithelium. Their peripheral ends penetrate the epithelial layer, and break up into brush-like terminations on its surface.

The kidneys lie dorsal to the pericardial cavity. The main secretory part is much pouched and lies on the posterior adductor muscle. It is connected with the posterior ends of the pericardial cavity by a very long, narrow duct, and with the exterior by a very long, larger duct which opens under the visceral ganglion.

In the adult *Teredo*, the sexes are separate. However, young individuals (1-4 cm. long) of *X. fimbriata* are very frequently hermaphrodite; in all such cases the sperms are always developed first, indicating that the species may be protandrous. The sexual duct is very short and is formed as an ectodermal invagination.

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EXPLANATION OF FIGURES.

General Reference Letters

an.	Anus.
a.a.	Anterior adductor Muscle
a.c.	Anal Canal.
a.g.	Anterior Ganglion.
ao.a.	Anterior Aorta.
ao.p.	Posterior Aorta.
a.p.	Posterior adductor Muscle.
a.pa.	Adductor Muscle of Palette.
a.r.v.	Afferent Renal Vein.
au.	Auricle.
b.a.	Afferent Branchial Vein.
b.e.	Efferent " "
b.s.	Flood Space of Gill Lamina.
by.	Byssus.
b.g.	Branchial Groove.
c.	Cerebral Ganglion.
c.c.	Cerebral Commissure.
c.s.	Crystalline Style.
ce..	Caecum of Stomach.
ce'.	Secondary Caecum of Stomach.

- c.h. Cerehalic Hood of Mantle.
- c.p. Cerebro-pedal Connective.
- c.v. Cerebro-Visceral Connective.
- d.D. Duct of the Gland of Deshayes.
- d.a. Dorsal Artery.
- d.k. Dorsal pivotol Knob of the Shell.
- ep.c. Epibranchial Cavity.
- ep.ca. " Canal.
- e.s. Exhalent or Anal Siphon.
- f. Foot.
- f.c. Frontal Cells of Gill.
- g. Ctenidium or Gill.
- g'. Anterior Gill Filaments.
- g.a. Ascending Limb of Gill.Filament.
- g.d. Descending Limb of Gill Filament.
- g.du. Genital Duct.
- g.D. Gland of Deshayes.
- gl.ep. Gland Cells of Epidermis.
- g.o. Genital Organ.
- i. Intestine.
- i.f.j. Inter-filamentar Junction of Gill.
- i.l.s. Inter-laminar Spaces of Gill.
- i.s. Inhalent or Respiratory Siphon.

- k. Kidney.
- k.a. Afferent Tube of Kidney.
- k.e. Efferent Tube of Kidney.
- l. Liver. l.d. Liver Duct.
- l.c. Lateral Cells of Gill.
- lr.c. Latero-frontal Cells of Gill.
- lig. Shell Ligament
- m. Mantle.
- m.c. " Cavity.
- mu. Muscle Fibres.
- o. Mouth.
- oe. Oesophagus.
- o.n. Osphradial Nerve.
- os. Osphradium.
- ot. Otolithic Vesicle.
- ov. Ovary.
- p. Pedal Ganglion.
- pa. Palette.
- p.c. Pericardial Cavity.
- p.gl. Gland Cells of Foot.
- pl. Pleural Ganglion.
- p.n. Pallial Nerve.
- p.p. Protractor Muscle of Palette.

- r. Rectum.
- r.f. Retractor Muscle of Foot.
- r.p. Retractor Muscle of Palette.
- r.s. Retractor Muscle of Siphons.
- s. Stomach.
- s.r. Supporting Rod of Gill Filament.
- s.s. Sheath of Crystalline Style.
- v. Visceral Ganglion.
- vl. Valve of Anterior End of Ventricle.
- v.c. Velar Cavity.
- ve. Ventricle.
- v.k. Ventral Pivotal Knob of the Shell Valve.
- v.m. Visceral Mass.

Explanation of Figures.

Fig. 1. Newly-attached larva of *X. fimbriata*. Sketched from life. The foot is shown fully extended. x 320.

Fig. 2. Newly-attached larva, from the right side.- The right shell, mantle and gills removed. The cells of the disintegrating velum are not represented. The foot not fully extended. x 320.

Fig. 3. Young "Ship-worm" of about three days attachment, from the ventral side. The shell is represented as transparent, to show the underlying gills on the sides of the visceral mass. x 250.

Fig. 4. Same stage as fig. 3, from the left side. The left shell, mantle and gills represented as removed. The double origin of the cerebral ganglion is still shown. The visceral ganglion and kidney still lie in front of the posterior adductor. The caecum fills the foot, and has crowded the crystalline style and intestine to the left side. x 250.

Fig. 5. Specimen of about one week in the wood. The worm-like form is becoming rapidly assumed. x 190.

Fig. 6. Same stage as fig. 5, ventral view. To show the arrangement of the gills and the extent of the visceral mass. x 190.

Fig. 7. Same as fig. 5, the left shell, mantle and gills

removed. The pericardial space with the included parts, was taken up a position posterior to the adductor muscle. The secondary caecum of the stomach has been formed. The gills project beyond the visceral mass. x 190.

Fig. 8. Adult, from left side. The two extensions of the mantle over the shell shown on the dorsal side of the latter. The mantle also extends over the posterior margin of the shell for a short distance. The siphons are represented as fully extended, but the palettes not quite fully retracted. The mantle extends over the bases of the palettes as a collar. The attachments of the muscles of the palettes and siphons are shown. The drawing was made from a slightly contracted specimen 10 cm. long.

Fig. 9. Same as 8, the mantle removed to its line of attachment dorsally, at the two ends, to the midline.

Fig. 10. Adult, anterior half of the body, with the left shell valve, mantle and gill removed, and the pericardial cavity laid open. Half of the posterior adductor removed.

Fig. 11. Right, and fig. 12, left shell valves of newly-attached larva, internal view. The rudimentary apophyses are shown below the teeth. x 220.

Fig. 13. Shell of newly-attached larva, end view. x 220.

Fig. 14. Shell of "Ship-worm" that has been in the wood

about one day, front view. The first row of teeth, apophyses and pivotal knobs have been formed. The shell capes at both ends. x 220.

Fig. 15. Left shell valve of specimen about 1 mm. long. Oblique view. The larval shell still shown. x 220.

Fig. 16. Left shell-valve of specimen 5 mm. long. x 15.

Fig. 17. Left shell-valve of adult. x 15.

Fig. 18. Front view of shell of adult. x 15.

Fig. 19. Internal view of right valve. x 15.

Fig. 20. Left palette of specimen 5 mm. long. x 140.

Figs. 21 and 22. Diagrams of the posterior end of body of adult, left side, to show the arrangement of the siphons and palettes, and their muscles. In fig. 21 the siphons are represented as extended, the palettes as retracted; in fig. 22, the siphons are represented as contracted, the palettes as protracted.

Fig. 23. Dorsal gland of the posterior part of the mantle. Section of whole gland of specimen 5 mm. long. The letters are placed in the epibranchial cavity. x 350.

Fig. 24. Sagittal section of a newly-attached larva. The very large glands of the foot occupy a large part of the mass of the latter. A large quantity of material derived from these glands lies adjacent to the byssus gland. The

disintegrating cells of velum, some of which have been eaten, are not represented. x 560.

Fig. 25. Transverse section of larva. From a specimen in which the foot was more protracted than in fig. 24. The ventral mantle edge is filled with cells gorged with material, evidently for the rapid growth of the shell during its transformation. x 560.

Fig. 26. Horizontal section of specimen in which the cavity of the velum was partially obliterated. On the left side the contents of the gland of Deshayes are shown; on the right side, the duct. x 560.

Fig. 27. Transverse section of a specimen 1 mm. long, to show especially the extent and relations of the gland of Deshayes. x 250.

Figs. 28-35. A series of transverse sections of a specimen 10 cm. long, along the lines indicated in fig. 9. The drawings were made with the aid of a camera and afterwards touched up, though not essentially changed. The details of structure are semi-diagrammatic. The right side in the sections is on the left side of the observer. All x 30.

Fig. 28. Section through the posterior adductor muscle and cephalic hood. Tubular part of style sheath to the right side. Posterior aorta asymmetrical, on the right side.

Fig. 29. Section through the round typhlosole, canal-like anterior end of pericardial cavity and posterior end of the body of the kidney.

Fig. 30. Section through the large, posterior liver mass. Shows the distribution and character of the two different parts.

Fig. 31. Section through the large ventricle and the ovary.

Fig. 32. Section through the opening of the kidney into the pericardial cavity, the anterior ganglion and ends of the auricles. The two arrows from the right indicate the course of the water currents between the gill laminae; the one pointed dorsally, that of blood through the gill lamina. The number and distribution of the inter-laminar connections indicated by dots.

Fig. 33. Section near the posterior end of the visceral mass.

Fig. 34. Section to illustrate the structure in the long region between the visceral mass and muscular collar.

Fig. 35. Section through the "collar", palette handles and base of the siphons.

Fig. 36. Section of a palette handle and its sheath. The attachment of the ventral retractor muscle is shown. x 344.

Fig. 37. Lamina of gill of *T. navalis*, to show especially the distribution of the glands of Le-shayes, in which the elements are represented semi-diagrammatically. The arrows indicate the course of the water and blood currents over the lamina. The epibranchial cavity and the blood vessels are indicated by the letters which are placed in these spaces. x 312.

Fig. 38. Transverse section of three laminae almost in the line of the lower arrow in fig. 32. Two interlaminar junctions are shown. The two elements of the gland of Le-shayes are shown, both as to character and distribution. x 312.

Fig. 39. Tangential section of a gill to show the distribution of the inter-laminar junctions. x 312.

Fig. 40. Transverse section of three gill laminae, along the line shown in fig. 37, near the tip of the lamina, so as to show the interlaminar junctions on one side. x 360.

Fig. 41. Section of the three most anterior gill filaments at the side of the "hood". The one to the left is only a half filament. The letters are placed in the epibranchial canal. x 360.

Fig. 44. Group of cells from the branchial groove at the edge of the gill, showing the character of the ciliated cells

and the mucus cells among them. x 1900.

Fig. 43. Section of the branchial groove which connects the two parts of the gill. x 560.

Fig. 45. Section of the duct of the gland of Deshayes between the two parts of the gill. The epibranchial canal is shown to the left and the afferent branchial vein to the right. The great variety in the cells in the duct, is represented. x 1390.

Fig. 46. Section of two tubes of the gland of Deshayes, from a gill lamina. In the walls of the gill lamina are shown sections of the dendritic processes which penetrate among all portions of the glandular structures. x 1390.

Fig. 47. Coarser and fig. 48, finer portions of the dendritic processes from the gill lamina of *T. navalis* represented in fig. 37. The distribution and contents of these structures are represented in detail. x 1900.

Figs. 49-52. Four stages in the development of the structures of the second factor of the gland of Deshayes. x 1900.

Fig. 53. Heart of specimen 2 mm. long, dorsal view. Openings from auricle show through the walls of the ventricle. x 360.

Fig. 54. Heart of young adult. The anterior aorta is represented as turned to one side, and the auriculo-ventric-

ular valves as showing through the vessels of the ventricle. x about 20.

Fig. 55. Longitudinal section of the ventricle and vessels of a specimen 4 mm. long. The arrows indicate the course of the blood. The posterior adductor muscle, and the wall of the stomach represented in part. x 544.

Fig. 56. Longitudinal section of the anterior part of the ventricle and vessels of a specimen 10 cm. long. x 544.

Fig. 57 A, group of cells from the main portion of the style sheath, and 57 B, from the tubular portion. x 1150.

Fig. 58 A, group of cells from the liver which show the usual liver structure, and 58 B, from its modified portion. x 1150.

Fig. 59. Nervous system of newly-attached larva, showing the pleural ganglion still separate from the cerebral, and the visceral ganglia still wide apart. x 360.

Fig. 60. Nervous system of adult, dorsal view, except that the pedal ganglia are shown more from behind.

Fig. 61. Section of the osphradium, vertical to the surface, to show the structure of the osphradium and the two types of sensory cells, with their brush-like terminations. x 2420.

Fig. 62. Tangential section of the osphradium, to show

the distribution of the processes of the sensory cells along the nuclei of the epithelial layer. x 1900.

Fig. 63. Transverse section of the anterior ganglion and genital duct, to show the connection between the cerebro-visceral connective and anterior ganglion; and the origin of the sensory nerve and its distribution to the genital duct. Only a part of the sense organ was included in the section, which is from *T. navalis*, though it might represent *X. imbricata* equally well. x 544.

Fig. 64. Longitudinal Section of the genital duct, to show its extent and character, and the sense organ of the genital duct. The end of the ovary is shown, as also the folded kidney near its pericardial opening. X 544.

Figs. 65 and 66. Diagrams to show the relations of the ends of the kidneys, genital duct, pericardial cavity and visceral ganglion. Fig. 65 lateral, and fig. 66 dorsal view.

VITA.

Charles Peter Sigerfoos, son of Geo. W. and Nancy Sigerfoos, was born the 4th of May, 1865, near Arcanum, Ohio, where he lived and attended the public schools from 1872 to 1882. The fall of 1882 he entered the Ohio State University, where he spent two years in preparation, and four years in college, graduating in 1889 as S.P. Since graduating he has been occupied as follows: During the college years 1889-91, he was Assistant in Zoology and Comparative Anatomy in the Ohio State University; 1891-2, Instructor in Biology in the University of Virginia; 1892-3, a graduate student, and 1895-7, Assistant in Zoology and Embryology, in the Johns Hopkins University. During the summer of 1893, he was with the Johns Hopkins Marine Laboratory in Jamaica; and during the summers of 1894-5 at Beaufort, North Carolina. His chief subject has been Zoology, and his subordinate subjects Animal Physiology and Animal Pathology.

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